EVALUATING THE SCIENTIFIC SOUNDNESS OF PLANS FOR HARVESTING WOLVES TO MANAGE DEPREDATIONS IN MICHIGAN

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Summary

1) In 2013, the Michigan Department of Natural Resources (MI-DNR) began implementing a plan to harvest wolves. The stated purpose of the harvest is to reduce threats to livestock and human safety. While the MI-DNR has indicated that its plan is based on sound science, they have not presented any scientific evaluation of its plan. Moreover, we are unaware of any scientific evaluation of the prospects of success for the plan. Providing for sound science is required by Michigan law. Here, we provide a scientific evaluation of the prospects for successfully managing depredations in Michigan through the use of wolf harvesting.

2) This analysis indicates that realizing anything but trivial declines in depredations requires killing more wolves than would be appropriate. For example, reducing the expected number of farms affected by depredations each year by just a single farm, from 17.7 to 16.8, would require reducing wolf abundance, across Upper Michigan by ~20%, which would require harvesting approximately one out of every three wolves. That number of harvested wolves would be in addition to the wolves that will also be killed by poachers. Moreover, the spatial scale at which the MI-DNR plans to implement harvest will cause harvesting to be less efficient than suggested by statistics such as that reported in the previous statement.

3) Another anticipated result of the management plan is that harvesting wolves may alter wolves' behavior in a manner that would reduce livestock depredations. The available evidence does not support this expectation.

4) The ecological relationships associated with using harvest to manage depredations are characterized by considerable statistical and scientific uncertainty. In such circumstances, a scientifically sound management plan *must* account for the principles of adaptive management. Those principles include transparently: (i) specifying the goals of the harvest, (ii) using available data to assess the likelihood of realizing the specified goals given the planned management, (iii) specifying a plan to evaluate whether the actions were successful in realizing the goals, and (iv) specifying how actions are expected to be adjusted should the goal not be realized. The plan does not contain *any* of these basic elements. Analyses presented here strongly suggest that if the MI-DNR were to state an adequately specific goal, that such a goal would be extremely unlikely to be met through the harvest of wolves. These circumstances represent clear, unequivocal evidence that plans to harvest wolves in Michigan for the purpose of managing depredation are scientifically unsound. Fortunately, other effective means of managing depredations exist.

Background

One of the two reasons offered by the Michigan Department of Natural Resources (MI-DNR) for harvesting wolves is to reduce the number of depredations. The MI-DNR describes its plan for achieving this goal as being geographically targeted. In particular, the MI-DNR has identified three wolf management units (WMU) for 2013 where it will focus wolf harvesting (Fig. 1). For example, in WMU B 80 livestock on 11 farms were reported to have been killed by wolves between January 2010 and April 2013. In response, the MI-DNR plans to harvest 19 wolves in WMU B during Fall of 2013. They estimate that number of wolves to be harvested represents about 20% of the wolves living in WMU B. The intention is to reduce the number of depredations in WMU B. The MI-DNR has plans to harvest wolves at similar rates in WMU C to reduce depredations and in WMU A to reduce the number of humans making nuisance complaints about wolves.

The MI-DNR does not expect the total number of wolves harvested to affect the overall abundance of wolves in Upper Michigan, but it may reduce wolf abundance in the particular WMUs where wolves are hunted. In particular, they expect that a 20% harvest rate added to an estimated 15% rate of background mortality due to other human causes (e.g., poaching, lethal control, car collisions) would reduce abundance in the WMU by 25%. The MI-DNR also anticipates that harvesting wolves may alter the behavior of wolves living near livestock in a way that would reduce the number of depredations. Finally, the MI-DNR has implied that it will adjust rates of harvest up or down in each WMU over time in response to recent levels of depredation and in response to the perceived effect of previous harvests.

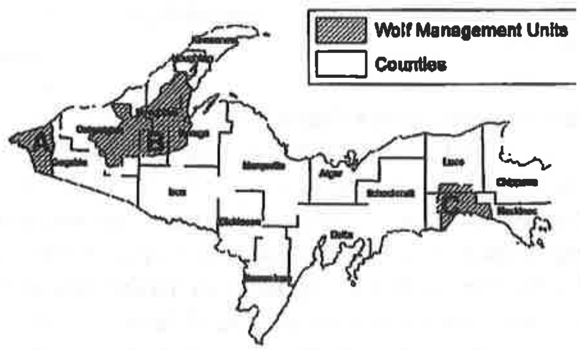

Fig. 1. Wolf Management Units for 2013.

The MI-DNR also stated that plans to harvest wolves are based on sound science. However, they do not cite what science they are referring to, and we are unaware of any science that supports critical elements of the plan. This document is a scientific analysis of the appropriateness of using a public harvest to manage depredations in Michigan.

Wolf abundance and depredation

The primary basis for the MI-DNR's expectation that wolf harvesting would reduce depredations appears to be the statistical tendency for the number of depredations to increase with wolf abundance. In particular, for the period 1996-2012, the statistical association between wolf abundance and number of depredations is highly significant ($p=6.6 \cdot 10^{-5}$; Fig. 1). Moreover, the proportion of variation in depredations that can be accounted for by wolf abundance is relatively high (i.e., $R^2 = 0.67$). Using Figure 1 to justify wolf harvesting as a means of controlling depredations requires assuming that the relationship is largely causal and not merely correlative. Sound-scientific reasoning indicates how that assumption is not fully appropriate and may simply be inadequate

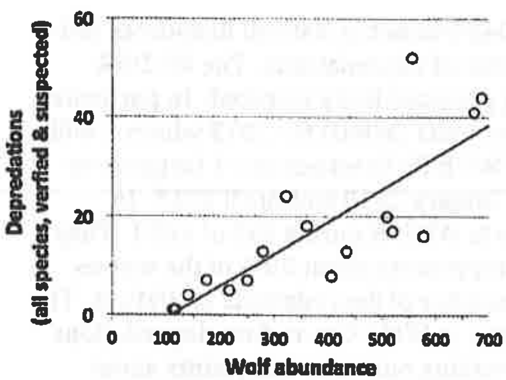

Fig. 2. Relationship between estimated wolf abundance and depredations in Upper Michigan, 1996-2012.

(see below). Nevertheless, even if one were to fully grant the assumption, the relationship in Figure 1 is still an inappropriate basis for thinking that wolf harvest is a scientifically-sound means of managing depredation. The problem with the relationship in Figure 1 is revealed by a more thorough analysis of the statistical uncertainty characterizing that relationship.

To provide context for such an assessment, consider that 41 depredations (all species, verified and suspected) were reported in 2012, a year during which there were also approximately 675 wolves. The simple linear regression line in Figure 1 indicates that the *expected* number of depredations, given this wolf abundance, is 36.8.

The foundation of this analysis is appreciated by observing that the realized number of depredations in a particular year (represented by the circles in Figure 1) typically differs, and often by a great amount, from the expected number of depredations in a particular year (represented by the regression line). For this reason, the regression line is, by itself, an inadequate indication of the relationship between wolf abundance and the actual, observed number of depredations. Critical insight rises from confidence intervals in the number of depredations, for any given level of wolf abundance. For example, when wolf abundance is 675, then the 80% confidence intervals for the number of depredation is [23.3, 50.3]. The approximate meaning[1] of this statistic is: When there are 675 wolves, one can be 80% confident that the realized number of depredations will be somewhere between 23.3 and 50.3. Put another way, when there are 675 wolves, there are as likely to be 23.3 or fewer depredation as there are to be 50.3 or more depredations. From a management perspective, this is a remarkably wide range of depredations.

Suppose, simply for the sake of illustration, that a planned harvest would reduce overall wolf abundance by 10%, say from 675 to 608 wolves. The regression line in Figure 1 indicates that the expected number of depredations would decline from 36.8 to 32.4 depredations. However, the statistical uncertainty and confidence intervals that correspond to this relationship are considerable. Consequently, there is a considerable chance that depredations would increase, just by luck, with a 10% decrease in wolf abundance (Table 1). Table 1 shows what can be expected, if Figure 1 depicts a purely

[1] The technical interpretation of a confidence interval is more nuanced than what is stated above. Nevertheless, it captures the practical meaning of those confidence intervals. Furthermore, by the conventional standards of statistics, an 80% confidence interval represents a low level of confidence; a conventional level of confidence is 95%. Selecting that level of confidence would have resulted in even greater uncertainty about the number of realized depredations (i.e., [15.4, 58.2]). For purposes of illustration, however, we will continue to use 80% confidence intervals, which give the appearance of greater certainty (i.e., narrower, more precise intervals) than would 95% confidence intervals.

causal relationship, for declines in depredation, given various reductions in wolf abundance.

That table indicates, for example, that reducing wolf abundance by 20% results in only a 56% chance of realizing a decline of 7 (or more) depredations each year[2]. That is, the probability of realizing a reduction in depredations by reducing wolf abundance by 20% is essentially equivalent a coin toss (i.e., 0.50). For context, there is also a coin toss's chance (50%) of realizing a reduction in depredations even if no wolves are harvested.

TABLE 1. EFFECT OF REDUCING WOLF ABUNDANCE ON THE NUMBER OF DEPREDATIONS.

Reduction in wolf abundance	Expected number of depredations	80% Confidence Interval	Probability of realizing an *increased* number of depredations, in spite of reduced wolf abundance	Probability of realizing a *decrease* in depredations from 36.7 to less than or equal to 30
0% (675 wolves)	36.7	[23.3, 50.3]	0.50	0.31
10% (608 wolves)	32.4	[19.3, 45.5]	0.37	0.43
20% (540 wolves)	28.0	[15.2, 40.9]	0.26	0.56
30% (472 wolves)	23.6	[11.0, 36.3]	0.16	0.69
40% (405 wolves)	19.2	[6.7, 31.8]	0.09	0.79

The calculations in Table 1 assume that the variance in number of depredations is constant with respect to wolf abundance. Figure 1 suggests otherwise. Variation in depredations appears to increase considerably with increased in wolf abundance. Accounting for that increase would almost certainly add to the uncertainty that is portrayed in Table 1.

If managing losses due to depredation is important, paying for the lost economic value of seven head of cattle (on the order of $2,500, total[3]) would be more reliable and effective than harvesting wolves. Regardless, the available evidence clearly indicates that reducing wolf abundance to manage the number of depredations would be remarkably inefficient and ineffective.

This conclusion is also supported by analyses (not shown) that focus on cattle only and dogs only, rather than treating all depredations together (as depicted in Figure 2). The analysis represented by Figure 2 and Table 1 also estimated wolf abundance in 2012 by interpolation of estimates for 2011 and 2013. If data from 2012 is omitted, the relationship between abundance and depredation is characterized by *more* statistical uncertainty than indicated by Table 1.

Forecasting ecological events

One aspect of these results deserves explanation. In particular, how can the statistical relationship between wolf abundance and depredations be so highly significant and

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[2] See *Adaptive Management and Success Criteria* (below) for a discussion of what would count as a meaningful decline in depredations.

[3] This value is estimated from Table 5 of Roell et al. (2010).

with a relatively large R^2 ($p = 6.6 \cdot 10^{-5}$, $R^2 = 0.67$; Fig. 2); yet, at the same time, the prospects for realizing reductions in depredations are so poor? The explanation for this circumstance follows:

First, statistical significance is not, in general, an indication for the ability to make adequately precise predictions about future events. Statistical significance is *not* an indication that reducing, even substantially, the predictor variable (wolf abundance) will result in realizing an adequate reduction or any reduction in the response variable (depredations). Realizing that kind of reduction requires a steeper slope *and* higher R^2 than were observed in Figure 1, provided, of course, that the relationship in Figure 1 is purely causal.

Also, if the R^2 observed in Figure 1 seems large, that is only in comparison to informal standards for evaluating whether one ecological parameter has in the past had some connection to another ecological parameter. The standard for concluding that one ecological variable (depredations) can be adequately managed or controlled by manipulating another variable (wolf abundance) is different and represented by the calculations in Table 1. By those standards, the R^2 observed in Figure 1 is not large.[4]

In other words, the observed R^2 is large compared to many ecological relationships that have been observed in nature. However, nature is impressively stochastic and ecological phenomena are the result of many factors operating simultaneously. As a result, R^2 values of the size observed in Figure 1 satisfy the intellectual curiosity of ecologists aiming to understand whether two ecological variables have, in the past, been connected in some way. Nevertheless, the standards for developing a *general understanding of past events* are not the same as the standards for making adequate *predictions of the future*. Because ecologists spend most of their time understanding the past, rather than making formal predictions of the future, their

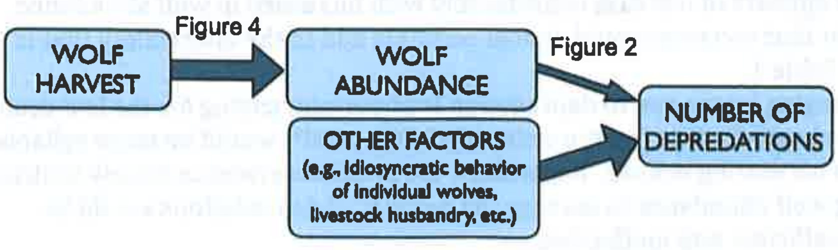

Fig. 3. The statistical relationship between wolf harvesting and number of depredations is comprised of two sequential statistical relationships, each characterized by considerable statistical uncertainty. The first is the relationship between harvest rate and wolf abundance (see Figure 4). The second relationship is between wolf abundance and number of depredations (see Figure 2 and Table 1). The potential for harvest to reduce depredations by altering the behavior of wolves is discussed below, in Wolf Harvesting and Wolf Behavior. This conceptual model also highlights that the number of depredations is influenced by more than wolf abundance, and there is no scientific evidence to suggest that abundance is the most important, or even an important, causal determinant for the number of depredations (see for example, Treves et al. 2011).

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[4] For additional context, the value of $R^2 = 0.67$, reported in Figure 2, means that a third of the variation in depredations is not accounted for by wolf abundance.

intuition for the latter tends not to be as reliable. This is why the formal calculations in Table 1, which represent the standards for making formal predictions, are so important.

Wolf abundance and harvest rate

Attempting to manage depredations by harvesting wolves is a two-step process and involves two statistical relationships (Fig. 3). The second relationship is described in the previous section. Further uncertainty for the effect that harvesting wolves would have on depredations is revealed by considering that first ecological relationship, which is the relationship between harvest rate and wolf abundance (Fig. 4).

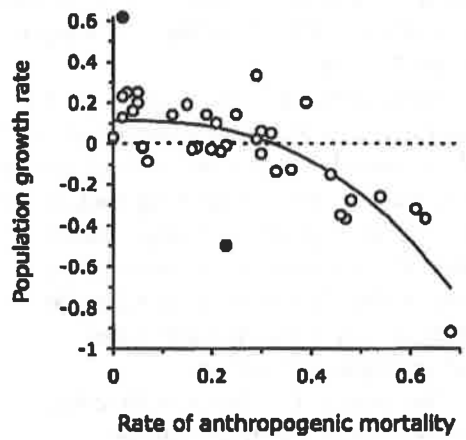

Fig. 4. Relationship between rate of anthropogenic mortality and population growth rate for populations of wolves living at various sites throughout North America. The filled circles are outliers. The curved line is the best fitting non-linear model ($y=0.114 - 2.284x^{2.658}$; $R^2=0.71$; $p<0.01$). Data are from Adams et al. (2008). Anthropogenic mortality includes harvest, poaching, lethal control, and car collisions.

The relationship in Figure 4 can be used as a basis for predicting how various rates of harvest are expected to affect wolf abundance. Suppose the intention is to reduce abundance by 20% (see the scenario implied by Table 1). That reduction in abundance corresponds to a growth rate of –0.20 (y-axis of Figure 4). An expected growth rate of –0.20 corresponds to killing 47% of the wolves in an area (see Appendix B).

Moreover, those statistics represent an incomplete perspective because they do not account for the statistical uncertainty characterizing the relationship between mortality and population growth rate in Figure 4. Because of this uncertainty, killing 47% of the wolves in an area is also associated with a twenty percent chance of reducing wolf abundance by *more* than 35%, and a twenty percent chance of reducing wolves by less than 6%. In other words, the *best* chances for realizing the desired outcome would still be accompanied by a forty percent chance of realizing an undesirable outcome (i.e., either reducing wolves too little to make a difference, or reducing them too much). The uncertainties described above would be amplified by limited knowledge of how rates of poaching fluctuate over time and in response to the opportunity for citizens to harvest wolves legally.

The MI-DNR believes it is taking a conservative approach to this statistical uncertainty. In particular, they are planning for the rate of anthropogenic mortality in the WMUs to be 0.20 (harvest rate) plus 0.15 (other sources of anthropogenic mortality, such as poaching), which would yield a total rate of anthropogenic mortality of 0.35. That rate of mortality corresponds to an expected population decline of 2.6%. These calculations differ considerably from the expectations reported by the MI-DNR (i.e., they expect a 25% decline in abundance within the WMUs). That difference is of significant concern. Nevertheless, it is not possible to evaluate why the MI-DNR expectations differ because they have not presented any scientific evidence (i.e., statistical analysis) to support their expectations.

This approach is not conservative by the standards to which management should be judged, because killing wolves at that rate has essentially no chance of reducing abundance enough to have any effect on depredations. The scientific soundness of management depends on the likelihood of realizing the management goals in response to the planned management actions.

The inherent problem with using wolf harvesting as a tool to manage depredations is that too many wolves have to be harvested to realize anything but a trivial decline in depredations. Planning to kill too few wolves to have any appreciable effect on depredation is not a conservative plan; it is a planned failure. The circumstances would be different if the cost of the planned management actions were negligible, but they are not. Rather, the costs of the planned management actions are considerable. That is, considerable cost is incurred for planning to kill dozens of sentient creatures with little or no hope of realizing the purpose for that killing[5].

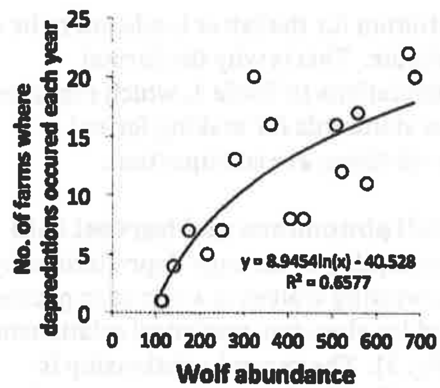

Fig. 5. Relationship between wolf abundance and number of farms affected by depredations in Upper Michigan, 1996-2012. These include depredations of all species, verified and suspected.

Number of affected farms

Concern for the number of farms affected by depredations each year is similar in importance to concern for the total number of depredations occurring each year. Moreover, the relationship between wolf abundance and the number of affected farms is statistically significant ($p<0.01$), and wolf abundance explains a relatively large portion of the variance in the number of affected farms ($R^2=0.66$; Fig. 5).

However, reducing wolf abundance by 10% from 675 to 608 reduces the expected number of affected farms by just a single farm, from 17.7 to 16.8. Reducing the expected number of affected farms by four (to 13.2) would require reducing wolf abundance by 40%, from 675 to 405 wolves.

The statistics in the preceding paragraph focus on expected reductions in the number of affected farms, and do not account for the difference between expected and realized outcomes. Because the confidence intervals for the number of affected farms is relatively large[6], one can expect considerable differences between expected and realized outcomes. For example, after reducing wolf abundance by twenty percent

[5] That wildlife managers be concerned with this cost is not a standard that we impose on wildlife management; it is a standard imposed by wildlife managers on themselves. For example one of the seven principles of the North American model of Wildlife Conservation is that wildlife not be killed for frivolous reasons. Hunting wildlife without realizing the intended purpose of that killing is to kill for a frivolous reason.

[6] The 80% confidence intervals for the number of affected farms, given 675 wolves is [12.0, 23.5].

there is a 39% chance that the realized number of affected farms would actually increase[7]. The available evidence clearly indicates that using wolf harvest as a tool to manage the number of affected farms would be remarkably inefficient and ineffective.

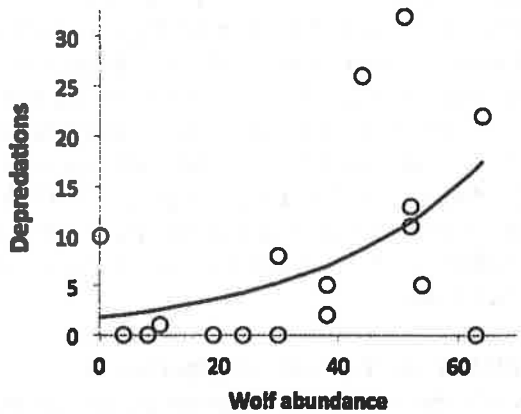

Fig. 6. Relationship between wolf abundance and number of depredations within wolf management unit B (see Figure 1), 1995-2012. Depredations include all species, verified and suspected.

Spatial scale

The analyses associated with Figures 2 and 5 are based on data gathered at a relatively large spatial scale (i.e., all of upper Michigan). By contrast, the MI-DNR plans to manage the depredation through wolf harvesting at a smaller spatial scale. Nevertheless, the analyses presented here, representing larger spatial scales, are relevant for two reasons.

First, the larger spatial scale highlights the magnitude of reduction in depredation to be expected if the MI-DNR were to apply management at the large scale. However, this is not their intention. Consequently, the expected magnitude of the reductions in depredations will be even smaller than what is reported here.

Second, for the application of harvesting at a smaller geographic scales to be sensible, the relationship between wolf abundance and the number of depredations would have to be considerably stronger and more precise than what is observed at the larger spatial scale. This, however, appears not to be the case. For example, the relationship between wolf abundance and number of depredations within WMU B (Fig. 1) is weaker than what is observed at the larger spatial scale (Fig. 6). In particular, the Poisson regression model depicted in Figure 6 accounts for only 21% of the observed variation in depredations, less than a third of the variation predicted at the larger spatial scale of the entire Upper Peninsula[8]. Consequently the results presented above, in *Wolf abundance and depredation*, are overly optimistic.

The reason for the weaker relationship at the smaller spatial scale is that the number of depredations is a highly stochastic event that depends on many variables. At smaller spatial scales the idiosyncratic nature of depredations dominates. Only at larger spatial scales does one see the kind of relationships depicted in Figures 2 and 5. This idiosyncratic nature is why depredations are not well managed by a crude tool

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[7] The result is based on calculations like those depicted in Table 1.

[8] In particular, the relationship between abundance and depredations across the Upper Peninsula is characterized by an R^2 of 0.67 (see Figure 2). That statistic indicates that abundance accounts for 67% of the variation in depredations (at the scale of the Upper Peninsula). In the context of Poisson regression, the comparable statistic is not R^2, but is called, a prediction error. The prediction error for the model depicted in Fig. 6 is 0.21. In other words, the relationship between abundance and depredation at the scale of a WMU is characterized by much more statistical uncertainty than what is observed at the larger spatial scale of the entire Upper Peninsula.

such as wolf harvesting, even when applied at relatively small spatial scales. Rather, depredations in a place like Michigan, where depredation events are relatively uncommon (compared to western states), are effectively managed only through more targeted methods like those which have been employed by the MI-DNR in the past.

Another concern about planning to focus harvesting within particular WMUs is that some portion of the harvest will, nevertheless, be comprised of wolves that are reported to have been killed within a WMU, but are actually killed outside the WMU. That expectation means that the harvest will be less geographically focused than intended. This circumstance should also be expected in spite of diligent law enforcement.

Wolf harvesting and wolf behavior

An advocate for managing depredations through wolf harvesting might insist that doing so is sensible not because of the relationship between wolf abundance and depredations, but instead because of the expected effect of harvest on the behavior of surviving wolves. That is, some believe that harvesting wolves should be expected to change their behavior in a way that would reduce depredations.

We searched the scientific literature and spoke with several knowledgeable colleagues and were unable to find any scientific evidence to support this claim. For example, we are unaware of any wildlife management agency that implemented and evaluated a harvest primarily for the purpose of making a predator behaviorally averse to depredation. If the MI-DNR has scientific evidence to suggest otherwise, they should share that knowledge. To date, they have not.

Moreover, existing knowledge of wolf behavior provides several reasons to believe that the planned harvest will not alter the behavior of wolves in a way that would reduce depredations.

First, no evidence exists to suggest that wolves have, in general, the capacity to know the difference between poaching, lethal control, or regulated harvest. And, humans have already been killing wolves in Upper Michigan on a regular basis for several wolf generations. There is no need to conduct a management experiment to see if killing wolves will affect their behavior. We have already been conducting that experiment and have observed its effects. Any behavioral modification attributable to the lethal removal of wolves are already be in place.

Second, there is a mismatch between the time of year when harvesting would occur and the time of year when most depredations occur (Figure 7). The cognitive abilities of a wolf include the capacity to understand when and where threats to their lives occur. There is little doubt that wolves are intelligent enough to quickly learn that a risk of being harvested in November and December is not a threat to their killing livestock in spring and summer, which is the time when most depredations occur[9].

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[9] Every hunter who has scouted the behavior of a deer prior to hunting season is impressed by their capacity to understand where and when their lives are at risk of being killed by a human. If deer are capable of such an ability, certainly wolves are too. Extensive research indicates that carnivores, including wolves, tend to adjust their behaviors match the time and place where human threat exists (van Schaik and Griffiths 1996, Gibeau et al. 2002, Beckmann and Berger 2003, Bunnefeld et al. 2006, Chavez and Gese 2006, Larrucea et al. 2007, Hebblewhite and Merrill 2008, Sweanor et al. 2008).

Third, a likely effect of harvesting wolves within any WMU is to increase the number of wolves immigrating into the WMU. These immigrating wolves that have not been acculturated (aversively conditioned) to living in areas with livestock are more likely to kill livestock. For this reason, harvesting could exacerbate losses to livestock (see also Bangs and Shivik 2001; Treves and Karanth 2003; Treves and Naughton-Treves 2005). The same conclusions results from considering other expected effects of harvest on wolf populations (i.e., Brainerd et al. 2008; Wallach et al. 2009; Rutledge et al. 2010).

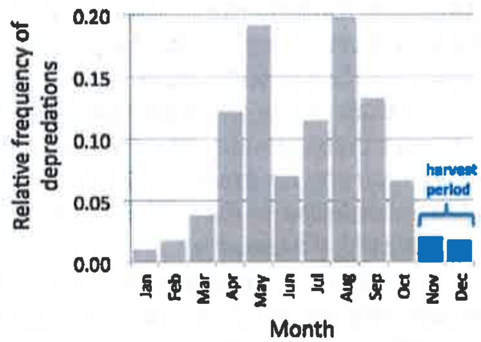

Fig. 7. Seasonal occurrence of depredation events in Michigan, 1996-2012. Only 3.8% of depredations occur during the planned harvest season.

According to a July 2013 report in the Minneapolis Star Tribune, Dan Stark of the Minnesota DNR believes that existing evidence indicates that declines in complaints about wolf depredation in Minnesota during the previous year are "likely explained" by the targeted removal of wolves (by state and federal trappers) that had been living near farms and threatening livestock, and not the wolf harvest (Smith 2013). Other forthcoming analyses also suggest that the number of depredations may have increased in response to harvesting (Kunkel 2013, see also Musiani 2013).

Frequency of estimating wolf abundance

The MI-DNR has stated that the planned harvest "*is extremely unlikely to impact the overall UP wolf population size. We expect the population trajectory to remain unchanged despite the harvest recommended in this memo.*" (MI-DNR 2013). The concern with this expectation is that the MI-DNR is planning to estimate wolf abundance no more than once every other year. Significant declines in abundance are difficult to detect in a timely manner when abundance is estimated less than once a year. A scientifically sound harvest plan would include an adequate statistical assessment of the MI-DNR's ability to detect declines in wolf abundance should they occur. No such assessment has been provided.

This concern is well justified because conducting such an assessment is not difficult, and the risk of realizing an unexpected, undesirable decline is not hyperbolized. For example, the state of Minnesota also planned to harvest wolves in a way that would not "have a major influence on overall wolf numbers" (Smith 2013). Despite their expectations, they have been surprised. In 2013, Minnesota suddenly and drastically reduced hunting quotas by 50% upon realizing that wolf abundance had declined by 24% during a five-year period, between 2008-2012. The causes for that decline, and the influence of harvest on that decline, are not adequately understood.

Adaptive management & success criteria

Plans to harvest wolves for the purpose of managing depredations are characterized by considerable scientific uncertainty, to say the least (e.g., Table 1). In such circumstances, the scientific soundness of a plan *requires* the proper application of adaptive management. The MI-DNR has implied that it would adopt such principles, when it wrote, for example, (MI-DNR 2013), "*...we will evaluate and make recommendation to the NRC to adjust the WMUs, bag limits, and harvest targets periodically, if necessary.*"

Adaptive management is not an informal, imprecise sentiment whereby some actions are implemented and then adjusted "if necessary," without specifying in any way what "if necessary" means. For example, would a decline in depredations indicate that the hunt had been effective and no longer necessary? Or would a decline indicate that the hunt has been effective and thereby justify the need for more hunting to further reduce complaints?

The application of adaptive management requires:

- *(i)* *Transparent articulation of measurable goals.* In particular, the goal is to reduce depredations by what amount? Answering this question is critical because it is unreasonable to think that depredations will be reduced to zero, and it is also unreasonable to consider a harvest successful if it reduced depredations by, say, one or two depredation events per year.
- *(ii)* *Transparent use of existing data to evaluate the likelihood that planned management actions would result in achieving management goals.*
- *(iii)* *Transparent specification, in advance, of how one would expect to alter management actions, should the goal not be achieved.* These expectations may change over time, but the development of some kind of *a priori* expectations is vital.

Scientifically-sound management and the principles of adaptive management also require the transparent specification of plans for how future outcomes of the management actions will be analyzed. In particular, suppose that wolves are harvested and depredations decline. How much of a decline would have to be observed to conclude that the decline was not simply due to chance variation? For example, suppose depredations declined from the 41 observed in 2012 to 25. A decline of that magnitude would be consistent with past variation[10] and would not, according to the principles of sound science, be attributed to harvest. The statistical uncertainty associated with the number of depredations indicates the need to think carefully in advance about how harvesting's effect on depredations will be evaluated.

Moreover, wolf abundance is not the only factor affecting depredations. For example, in Minnesota, a significant decline in depredations during the past year is thought to be caused, not by the wolf harvest, but by the previous year's relatively severe winter, which made it easier for wolves to survive on wild prey (Smith 2013). A similar relationship is also well documented in Michigan (Edge et al. 2011; see also

[10] This is because the 80% CI for the number of depredations when there are about 675 wolves is [23.3,50.3]. See also Table 1.

Mech 1998). A scientifically sound plan would address the concern that declines in depredation can be caused by factors other than wolf abundance.

This concern is highlighted by observations from western states that experience depredations by wolves. In particular, the frequency of depredations has declined in all three states (Idaho, Montana, and Wyoming). Moreover, the greatest declines were in Wyoming where there has not been any harvesting. That pattern is consistent with two concerns: (i) harvesting is not an important cause of declining depredations and (ii) harvesting may even work against processes that reduce depredations (as suggested by Wyoming experiencing a greater reduction in depredations than Montana and Idaho).

For emphasis, these are not optional elements of management, if management is to be based on sound science. They are required. Plans for harvesting wolves in Michigan do not include any of these elements. While addressing these issues requires considerable care and thought, they are not onerous or expensive. Failure to provide those elements is unequivocal evidence that those plans are not based on sound science, and consequently do not meet the requirements of Michigan state law (i.e., Proposal G, 1996). The transparency afforded by these elements is also something that citizens deserve, both those who appreciate wolves as well as those who do not.

Conclusion

These circumstances would all be very unfortunate if there were no effective means of managing depredations. However, experience suggests that such means exist. For example,. (2011), which was authored by two MI-DNR biologists, states:

> *"Proven methods of limiting wolf predation include, management of birthing dates to limit exposure of young, herding vulnerable animals at night, combining herds as to not spread livestock across pastures, and locating birthing of young within barns... Use of an integrated management approach that emphasizes prevention methods and includes prompt responses to predation events and judicious use of compensation, may help decrease predation events, increase tolerance, and alleviate economic losses caused by wolf predations."*

Edge et al. (2011) makes no suggestion that wolf harvesting would be a sensible means of managing depredations. Rather, the data presented in Edge et al. (2011) and interpretation of that data provided by Edge et al. (2011) are suggestive that wolf harvesting would not be a sensible means of managing depredations. The analysis presented here in this document confirms what is suggested by Edge et al. (2011). The mutually reinforcing nature of this analysis and Edge et al. (2011) is ironic and disturbing insomuch as the MI-DNR asserts (without demonstration) that Edge et al. (2011) is significant scientific support for the idea that a wolf harvest is a sensible means of managing depredations.

The analysis presented here focuses on the assessment of depredations. Only the most modest extrapolation of this analysis is required to be deeply concerned that the MI-DNR plans to harvest wolves for the purpose of managing threats to human safety is also scientifically unsound. If necessary, we can provide such an analysis.

The analysis presented in this document provides clear indication that plans to harvest wolves as a means of managing depredations are not scientifically sound. While this is the case, the state of Michigan should refrain from harvesting wolves.

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APPENDIX A – Calculations in Table 1

The expected number of depredations and the 80% confidence intervals that are reported in Table 1 were calculated using standard regression formula and the R statistical software package. The R commands were:

```
> model<-summary(lm(depred~wolves, data=x))
> newdata = data.frame(wolves=c(675,608,540,472,405))
> predict(lm(depred~wolves, data=x), newdata, interval="predict", level=0.80)
```

The probability that depredations would increase between two subsequent years (i.e., the second from last column in Table 1) was obtained by calculating P(*X*>*Y*) = P(*X* – *Y* > 0), where *X* is the random variable representing the number of depredations in a year with 675 wolves; and *Y* is the random variable representing the number of depredations in the subsequent year, given the number of wolves specified by each row of Table 1 (e.g., 608 wolves). The probability distribution of *X* – *Y* is $N[\mu_X - \mu_Y, sqrt(Var_X + Var_Y)]$. The expected values for that distribution are derived from column two of Table 1. The variance of *X* and the variance of *Y*, which is the variance associated with observing a new observation, in the context of simple linear regression, are each equal to:

$$SE^2_{\hat{y}(x*)} = s^2_{Y|X} + SE^2_{\widehat{\mu_Y}|x^*} = s^2_{Y|X} + \sqrt{s^2_{Y|X}} \times \sqrt{\frac{1}{n} + \frac{(x^* - \bar{x})^2}{\Sigma n(x_i - \bar{x})^2}}$$

where, $s^2_{Y|X}$ is equal to (1/(*n* – 2)) × $\Sigma(e_i^2)$. The last column of Table 1 was calculated similarly, except those probabilities represent P(*X* – *Y* > 30 – 36.7).

APPENDIX B – Analysis of data in Figure 4

The data in Figure 4 are from Adams et al. (2008). Of the 41 observations used by Adams *et al.* (2008), five were from the wolf population on Isle Royale (1959-2006). In the analysis presented here, we represent the Isle Royale wolf population as a single observation ($m_a = 0$; $r = 0.03$), representing their population dynamics between 1959 and 2010, where m_a is the rate of anthropogenic mortality and r is the annual population growth rate. Adams *et al.* (2008) considered two other observations to be outliers ([$m_a = 0.02$, $r = 0.62$] and [$m_a = 0.23$, $r = -0.50$]; see Fig. 4). The residuals for these observations, in relationship to the best-fitting, non-linear model (see below), are 2.6 and 3.1 times the standard deviation of the residuals for the entire data set. The magnitude of these residuals suggests it may or may not be reasonable to consider these observations as outliers. We conducted a set of analyses omitting these observations, and another including them. Results for both analyses did not differ appreciably. Figure 4 depicts the result for the analysis excluding these observations.

We fit two models to the North American data, a simple linear model and $y = \beta_0 + \beta_1 x^{\alpha}$ where the superscript α represent a flexible way to allow for the possibility that the influence of m_a on r_t increases with increasing m_a. The non-linear model was unequivocally more parsimonious than the linear model. Specifically, the linear model was characterized by R^2=0.60, an Akaike Information Criterion value (corrected for small sample size; AIC$_C$) of –124.5, and an AIC weight of 0.01; and the nonlinear model was characterized by R^2=0.71, an AIC$_C$ value of –133.5, and an AIC weight of 0.99. The AIC weights indicate the non-linear model is 89 (=0.99/0.01) times more likely than the linear model. The results reported on page 7 of this document are the result of calculations associated with this best-fitting non-linear model. Additional details are available upon request.

Title: Killing wolves increased predation on domestic animals in the Great Lakes region, USA

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Abstract: Governments kill millions of wild animals annually to protect human interests. We evaluated two governments' interventions (lethal, non-lethal, and none) after 721 wolf-related threats to people or domestic animals. Threats generally increased after more wolves were killed, both locally and statewide within periods of 1–2 years. A small percentage of farms experienced benefits of lethal intervention but these were offset by significantly greater losses nearby, especially when wolves were killed after perceived threats rather than verified losses. The area of overlap between wolf territories and livestock-associated vegetation predicted annual losses better than did wolf abundance. Widespread perceptions that predator-killing is necessary but inadequate and that predator problems are worsening are parsimoniously explained by small-scale benefits offset by higher costs for distant properties.

key words: carnivore, conflict, cull, depredation, endangered species, euthanasia, lethal removal, livestock

Main text: People usually kill wild animals they perceive as threats, in hopes of preventing future harm. Worldwide, that tradition pervades modern wildlife management, especially for large predators living □near domestic animals (*1-4*). Recent work finds counter-productive increases in predation on livestock following the killing of cougars *Puma concolor* and gray wolves *Canis lupus* (*5, 6*). Reanalysis of early studies that killed coyotes to prevent sheep losses reveals several design flaws that undermine the claims of effectiveness (Supplementary Material 1). The best test of lethal management to date was a random-assignment experiment to prevent bovine disease transmission by badgers *Meles meles* in the U.K. Killing badgers raised disease transmission over large areas, which offset the modest, temporary gains enjoyed by a few properties from which most infected badgers had been removed (*7, 8*). Given the scale of wildlife-culling by some governments, concern is warranted, e.g., since 2000, the U.S. killed thousands of individuals from imperiled predator populations and >2 million native mammals (*9*). The U.S. is not alone (*2, 10, 11*). However, few studies of livestock predation compare the temporal and spatial aftermath of lethal interventions with alternatives.

We tested the hypothesis that lethal control prevented future depredations at four spatial scales and over intervals of days to two years. We analyzed three government interventions against wolf predation by Wisconsin and Michigan, USA. Interventions included the removal of 387 wolves, following damage to 1,766 domestic animals across both states from 1979–2014, as well as the local aftermath of lethal intervention, non-lethal deterrence, and no intervention at 166 farms (Supplementary Material 2). We addressed four unanswered questions. (i) Did the justifications for wolf removal affect the outcomes? (ii) Did different removal methods affect the outcomes? (iii) Were there threshold or nonlinear effects of lethal removal? (iv) Was wolf abundance predictive of losses at two spatial scales, and how did its growth respond to lethal removals? Our analysis was retrospective so we could not randomize the treatments experimentally. Nevertheless, having the history and locations of incidents and interventions (Figure 1A,B) permitted quasi-experimental, before-and-after comparisons for stronger inference than mere correlation.

Interannual comparisons across the states of Wisconsin and Michigan, USA: The number of verified incidents of wolf-related losses of domestic animals correlated positively to the number of wolves killed by the state governments in the previous year, whether measured in total, or by the components of depredation culling and other culling (Table 1, $p<0.0001$ in all cases). Translocation did not correlate significantly ($p>0.05$ in both cases). Although the positive associations suggest lethal intervention was not a remedy, other variables and temporal autocorrelation might confound the analyses because most rose steadily over time (Figure 1A,B).

The traditional assumption underlying lethal management is that property damages respond to the abundance of predators in the same year. A correlation with wolf population size was found previously in both states (*12, 13*). It exists in the present datasets as well (WI: number of wolf packs least-squares estimation LSE, Pearson r=0.890; average pack size r=-0.07; number of wolves r=0.877; MI: number of wolves r=0.886, we did not have number of packs for all years in MI). We pooled the two states' data to increase the power of a multiple regression using number of wolves in year t as a covariate alongside depredation culling and other culling in year t-1 (all variance inflation factors VIF < 3 to avoid misleading collinearity, adjusted r^2=0.72, p<0.0001). Depredation culling was not significantly associated with incidents the following year, after wolf abundance was controlled, whereas other culling was still positively correlated to incidents the following year (Table 2). When we included translocation, it had no significant association and the model performed less well (AICc=401). Nonlinear fits did not perform as well but the closest was logistic (Supplementary Materials 2).

Wolf abundance was not the strongest predictor of incidents. For 2000–2011 in WI, we had estimates of the geographic spread of wolves and the land-cover and snow-cover in the areas wolves inhabited (Supplementary Materials 2). Among six spatial predictors, the total wolf pack area under pasture, grassland, and hayfield was the strongest predictor of incidents the same year (r=0.803) and it outperformed the number of wolf packs (r=0.76) and number of wolves (r=0.77) for that span of years. The wolf pack area under pasture, grassland, and hayfield predicted future locations at high-risk of incidents with 91% accuracy (*14, 15*). The number of packs was too strongly collinear with the latter (VIF=33) to include them simultaneously in multivariate tests. So we compared the relative predictive strengths of wolf abundance and the wolf pack area under pasture, grassland, and hayfield, by standardizing both variables and comparing the variance explained and Akaike Information Criteria for small samples (AICc). Standardized pasture, grassland, and hayfield was stronger (adjusted r^2=0.88, AICc=101.4) than standardized number of packs (adjusted r^2=0.82, AICc=103.3). Incorporating pasture, grassland, and hayfield with depredation culling and other culling in those 12 wolf-years (VIF < 2.5 for all pairs, t=4.8, p=0.0013, p=0.0005) produced a similar, stronger model than one with wolf abundance (Table 2). It was similar except both depredation culling (slope=-0.6±0.2, t=-2.9, p=0.02) and other culling (slope=8.4±3.2, t=2.6, p=0.03) were significant. The effect of other culling was 14 times stronger than that of depredation culling expressed in terms of net change in incidents the following year. Had we not examined the wolf pack area under pasture grassland, and hayfield, we would not have detected the intended outcomes of depredation culling, small though it was. That led us to examine wolf abundance as a correlate and its response to lethal interventions the previous year.

Because lethal interventions and the wolf populations grew over time (Figure 1A,B), we tested if culling in year t-1 predicted the change in growth of the wolf population from year t-1 to year t (first differences). Counter-intuitively, first differences correlated positively to the number of wolves removed by depredation culling (n=53 wolf-years, r=0.57, p=0.011), other culling (r=0.19, p=0.44), translocation (r=0.33, p=0.67), or all removals (r=-0.54, p=0.022). For the number of packs in WI, the correlations were stronger (n=32 wolf-years, r=0.75, r=0.35, r=0.54, and r=0.78, respectively). The best multiple regression model included only a positive correlation between depredation culling in year t-1 and the number of wolves in year t (Table 3). Although before-and-after comparisons allowed stronger inference than mere correlation, they did not allow control over potentially confounding variables between sites and years. For that we turned to the analysis of the aftermath of interventions at fine spatial and temporal scales.

Recurrence of wolf-related incidents within Michigan: Our smallest scale of analysis was the section (a geopolitical unit of 1 $mile^2$ or 2.56 km^2) that never encompassed ore than one affected livestock operation. We excluded one outlier farm with >2 standard deviations more incidents than any other (Supplementary Materials 2). Of 149 remaining incidents 1998–2014, 17% recurred in the same section and year, 19% recurred in the same section later, and 64% incidents did not recur in the same section by the end of our study (Table 4). Interventions were not associated with the month of the incident, so delays to recurrence were neither biased by season (median test X^2=1.1, df=2, p=0.58) nor did delays change over the years of our study (Spearman correlation r_s=-0.12, p=0.14). The median delay to recurrence differed between interventions (X^2=9, df=2, p=0.011, Table 1) but this was not significant over the full span of a year (survival analysis: X^2=1.6, df=2, p=0.46, Figure 2A). At the larger scale of townships (a geopolitical unit of 36 $mile^2$ or 92.16 km^2), delays to recurrence and sample size diminished (Figure S1) as 16 original incidents in a section-year dropped out because they followed a prior incident in the same township-year (Table 4, Supplementary Materials 2, Figure S1). Of the 133 that remained as original incidents, 11% recurred in the same township and year, 26% recurred in the same township later, and 63% never recurred in the same township by the end of our study (Table 4). Delay to recurrence differed between interventions over a year (X^2=15, p=0.0006, Table 4, Figure 2B), although not in median delay (X^2=2.0, df=2, p=0.37) indicating a change in the pattern seen within section-years above. At the next larger scale (324 mile^2 or 829.44 km^2) equivalent to 9 contiguous townships, delay and sample size diminished as 30 incidents in a section-year dropped out as above (Table 4). Of the 119 that remained as original incidents, 16% recurred in the same year, 67% recurred in the same neighborhood later, and 17% never recurred in that neighborhood before the end of our study (Table 1). Interventions were similar in median delay (X^2=0.1, df=2, p=0.94) but significantly different over a year (X^2=16, p=0.0003, Figure 2C).

Delay was unrelated to the number of wolves removed (n=23, mean 1.5 sd 0.8 wolves removed. range 1–4 tested against delay for section: r_s=0.10, p=0.65, township: r_s=0.03, p=0.90; neighborhood: r_s=0.12, p=0.61) and unrelated to the interval before first removal (average 8 days sd 11; section: r_s=-0.01, p=0.96; township: r_s=-0.10, p=0.65; neighborhood r_s= -0.08, p=0.73). The number of lethal removals in a township was not related to the date of the first incident the following year (r=-0.10, p=0.70) but was significantly positively correlated to the number of incidents the following year in that same township (generalized linear model GLM with Poisson fit, log-link: r^2=0.13, p<0.0001, slope=0.25 ± 0.06, t=4.1, p<0.0001, AICc=237.6). We could not find confounding effects of other variables relating to intrinsic risk in townships (Supplementary Materials 2) but ran the same test again with incidents in year t-1 as a covariate (X^2=3.6, p=0.06). Lethal intervention in year t-1 remained significant (X^2=5.6, p=0.026) and model performance improved slightly (AICc=236.0). In sum, we could not detect variation in the timing of the first incident or a reduction in number of incidents in relation to the number of wolves lethally removed the prior year.

People in many regions argue that conflicts will escalate if wolf populations are not reduced, usually by hunting or liberal, lethal management (*16, 17*). Our results suggest lethal management displaced conflicts to other properties and increased losses of domestic animals especially when wolves were killed for perceived threats to people or domestic animals rather than actual damage. We detected both a local, temporary benefit of lethal intervention at the smallest scale and subsequent, higher costs expressed as more numerous and more rapid depredations at larger scales, when compared to no intervention. At its worst, lethal removal seems to have accelerated wolf-related losses of domestic animals by 5–18 weeks and affected 20–30% more farms up to 16 km from the site of lethal removal (Figure 2C). In this region, a wolf can cross such distances in a few days (*18*). Thus at small geographic scales benefits of lethal intervention were rare, brief, and local ((<8% of incidents in a section-year in Michigan, Figure 2A-C) and offset by higher costs on other farms in the vicinity. At the scale of the states of Wisconsin and Michigan, lethal intervention had a net cost of increasing domestic animal losses although 7% of lethal removals had a benefit between years when we controlled for the wolf pack area under pasture, grassland, and hayfield, Table 3). Our conclusions were reinforced by replicated findings for neighboring states that share the regional wolf population but implemented lethal removals independently (*19*). Usefully, the states differed slightly in lethal management strategies. In Michigan, 44% of lethal removals were motivated by health and human safety concerns or other non-damage events, whereas only 18% of those in Wisconsin were so motivated. This may reflect a false and inflammatory statement about threats to children outside a daycare, made by a Michigan state senator (http://www.mlive.com/news/index.ssf/2013/11/michigan_senator_apologizes_fo.html, accessed 20 January 2015). Killing wolves for perceived threats rather than actual damage resulted in 14 times higher adverse consequences and is therefore strongly counter-indicated. We also found hints of compensatory reproduction or breeding packs breaking into multiple smaller packs after lethal interventions. We recommend further examination of the reasons behind lethal intervention in other regions to explain additional variation in outcomes.

Our results help explain two long-standing phenomena in predator-killing. Lethal methods are popularly seen as effective responses yet after their implementation, predator problems are still believed to be rising (*20-23*). Surveys of Wisconsin residents indicated many believed killing wolves was the only way to prevent attacks on domestic animals and some believed they could teach wolves to fear people by killing many whenever encountered (*20, 23, 24*). Wisconsin and Michigan, the managers and stakeholders responded to seeing no effect of culling by escalating lethal interventions (*25, 26*). Indeed Michigan managers favored lethal removal more than did residents (*27*). These perceptions clash with a lack of scientific evidence for effectiveness of lethal methods (this study and Supplementary Materials 1). The popularity may stem from the few farms that experienced benefits from lethal removal of wolves followed by subsequent displacements of losses to other farmers who believed problems were on the rise (*23, 24, 28*), rather than the alternative that 'wolf-killing made it worse'. Managers might not make the connection unless they evaluate their interventions scientifically including monitoring the aftermath for predators and other farms over 2 years and hundreds of km^2. Although our findings apply specifically to the variety of lethal intervention practiced in these two states (USDA agents shooting live-trapped wolves on or near a property within 1 to several weeks after a verified loss of a domestic animal), we believe our evidence is more general when considered in conjunction with other studies (Supplementary Material 1). Concerns about the efficacy and counter-productive effects of lethal management extend beyond wolves to many large carnivores (*3-5, 29-32*).

Our findings contradict a long-standing idea that killing predators is the best way to prevent harm to domestic animals. The idea was supported by a single study in Canada that used poison bait to kill entire wolf packs (*33*) and early studies with flawed research designs (Supplementary Material 1). Our results extend more recent findings. Selective government culling and public hunting of Northern Rockies wolves were both followed by more livestock depredations the following year (*6*); also see corroborating evidence from Slovenia (*34*) and early years in Minnesota (*35*). We suggest the burden of proof now rests on proponents of lethal control to show a net effect of preventing livestock predation at scales beyond the affected farm and for periods longer than a few weeks. Evidence should include whether lethal management is more cost-effective than alternatives without displacing the problem to neighboring areas. Treating government interventions as an experiment might have revealed the phenomena described here and saved time, money, effort and animals' lives, both wild and domestic.

Although a clear cause-and-effect relationship might be observed when one shoots a predator in the act of attacking an animal, the same is not obvious for killing predators pre-emptively or long after an attack has occurred. Many wildlife managers traditionally assumed that predatory attacks on domestic animals were triggered by density-related competition between predators or the greater energetic needs of adults that have reproduced (*1, 36*). Yet in our study, predator abundance was a weaker predictor of domestic animal losses than the spatial overlap of predators with livestock-associated land covers. Therefore, policies focused on fiminishing predator populations are likely ot be counter-productive if the policy goal is to reduce real and perceived property loss. A more likely hypothesis is that lethal removal of predators y disrupts cooperative foraging groups, breaking social units into smaller more numerous breeding units, scattering individual survivors as loners and dispersers, or removing the wrong animals leaving culprits more numerous than non-culprits (*5, 31, 36-39*). Disruptions to cooperative breeding, hunting, and territoriality might lead pack-members to seek food independently or succumb to more numerous neighbors. Predators seeking food on their own may need more predictable sources and domestic animals on private properties would seem to be more predictable than wild prey both in space and time. We found such compensatory effects leading to more breeding packs and more domestic animal losses. We recommend the alternative of protecting domestic animals with better husbandry and preventing the spatial intermingling of predators with domestic animals through non-lethal methods. Nevertheless public and political pressures to allay fears for human safety and property will lead to calsl for killing regardless of the science. Indeed, some individuals will kill predators even if the government stops and prohibits the practice.

Our analysis did not account for poaching. Illegal killing of wolves occurs for a variety of reasons (*24*), and is notoriously difficult to measure (*40*). While fluctuating levels of poaching might be hidden within the data we analyzed, there is no research to suggest poaching would be more likely to succeed in preventing depredations than would government culling. Furthermore, if one assumes that poaching predators is more likely when the government does not (*19*), one would expect no difference between our treatments rather than the observed patterns of faster recurrence after lethal intervention. If on the other hand, poaching is more likely when the government implements lethal removal, as we hypothesized previously (*41*), then data on unobserved poaching mortalities become critical. Our results would be unaffected or even amplified if poachers take wolves because of perceived threats rather than verified damage.

Non-lethal methods are not exempt from our recommendation for experimental tests. Our results on non-lethal effects were equivocal. At farm levels, different sorts of non-lethal interventions were administered somewhat haphazardly and in mixed sets (i.e., cracker shells and flag fencing simultaneously or failed lethal intervention) without monitoring and produced intermediate delays to recurrence (Figures 2A-C). Moreover the non-lethal intervention considered most effective – human supervision or guarding (*3*) – was not reported. Statewide, translocation did not produce the adverse outcomes of lethal removals. Given that non-lethal methods are generally more politically acceptable, we recommend systematic, adequate investment in research and subsidies for livestock producers to install electrical fladry fencing or other deterrents that have been shown effective in many regions with many predators, when used correctly (*42-49*). In Sweden, wolf attacks on sheep have been practically eliminated on farms with appropriate electric fencing (*50*). Properly controlled experiments on all types of interventions are needed. Public trust depends on wildlife agencies adopting scientific approaches to management.

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Table 1. Univariate linear, rank, and nonlinear correlations between lethal interventions and verified Incidents of wolf-related loss of domestic animals in Wisconsin 1979–2013 and Michigan 1998–2014.

State	Lethal intervention in year t-1	Correlation with incidents in year t			
		Pearson r	Spearman r_s	Pearson r logistic transformation	Pearson r quadratic transformation
WI	All lethal interventions	0.58	0.87	0.77	0.78
	Depredation culling	0.43	0.72	0.62	0.52
	Other culling	0.66	0.77	0.78	0.85
	Translocation	-0.06	0.17	0.06	0.08
MI	All lethal interventions	0.50	0.78	0.71	0.65
	Depredation culling	0.23	0.52	0.12	0.22
	Other culling	0.69	0.75	0.72	0.69
	Translocation	-0.07	-0.04	-0.07	-0.07

Table 2. Multiple regression models predicting incidents in Wisconsin and Michigan combined.

Model with linear predictors	Beta	SE	t Ratio	p
(AICc = 398.5)				
Depredation culling in year t-1	0.1	0.2	0.9	0.38
(AICc = 396.9*)				
Other culling in year t-1	2.0	0.6	3.4	0.0013
(AICc = 405.3*)				
Number of wolves in year t	0.04	0.01	4.9	< 0.0001
(AICc = 463.8*)				
Intercept	-6.3	1.99	-3.4	<0.0001

* Stepwise removal of the predictor from the prior model; lower AICc indicates a better model

Table 3. Multiple regression models predicting the annual increment in wolf population size the following year, pooling Wisconsin and Michigan data

Model with linear predictors	Beta	SE	t Ratio	p
(AICc = 511)				
Translocation in year t-1	1.2	1.4	0.9	0.38
(AICc = 508.0*)				
State (AICc = 507.2*)	5.9	4.4	1.3	0.19
Other culling in year t-1	-1.4	1.4	-1.1	0.30
(AICc = 505.9*)				
Depredation culling in year t-1	1.3	0.4	3.0	0.0044
(AICc = 510.5*)				
Intercept	23	5	4.4	<0.0001

* Stepwise removal of the associated predictor from the prior model; lower AICc indicates a better model

Table 4. Incidents of wolf-related loss of domestic animals in Michigan 1998–2014 and the median delay until recurrence measured as the interval in days between an original incident and either a subsequent incident in the same vicinity that year or the end of that year. Vicinities were defined at three spatial scales (section, township, or neighborhood of townships). Excludes an outlier farm (Koski) with the most incidents and lethal removals.

Scale	Original incidents (N)	Delay (days)	Recurrence in the vicinity by the end of each year (end of the study)	Lethal intervention	Non-lethal deterrence	No intervention
Section	149	134	26 (28)	155 days (n=24)	156 days (n=16)	128 days (n=107)
Township	133	121	14 (34)	138 (n=24)	127 (n=14)	106 days (n=95)
Neighborhood	119	105	19 (80)	85 (n=21)	147 (n=13)	105 (n=85)

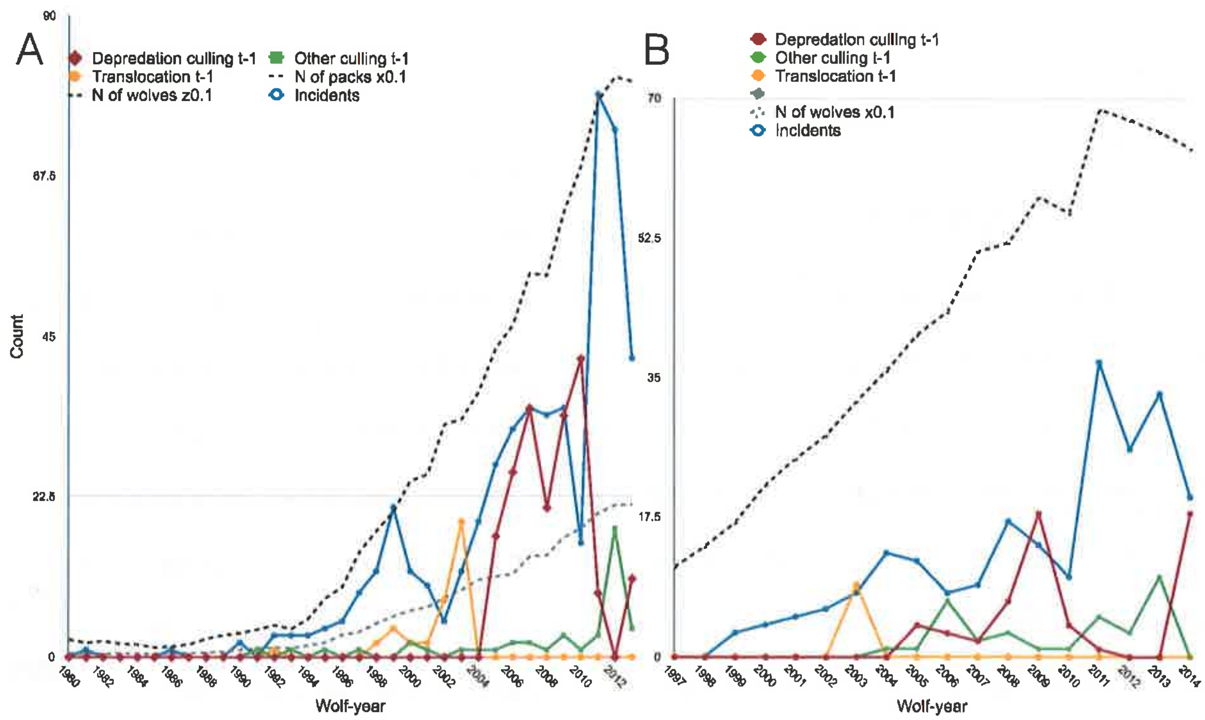

Fig. 1A. Wisconsin's interventions against incidents of wolf-related threats or losses of domestic animals, and changes in wolf abundance over time. Wolf-years span 15 April of year t-1 to 14 April of year t. Lethal interventions involved live-trapping and either trans locating wolves from private properties to wilder areas or killing wolves after livestock or pet attacks (depredation culling) or other culling (principally perceived threats to humans or property). Wolf abundance estimates were divided by 10 to fit the same y-axis as other variables and were depicted with dotted lines to connote they were estimated with error: minimum, late-winter wolf population estimate and the late-winter number of packs. V. same as A. except we did not have the number of wolf packs for every year.

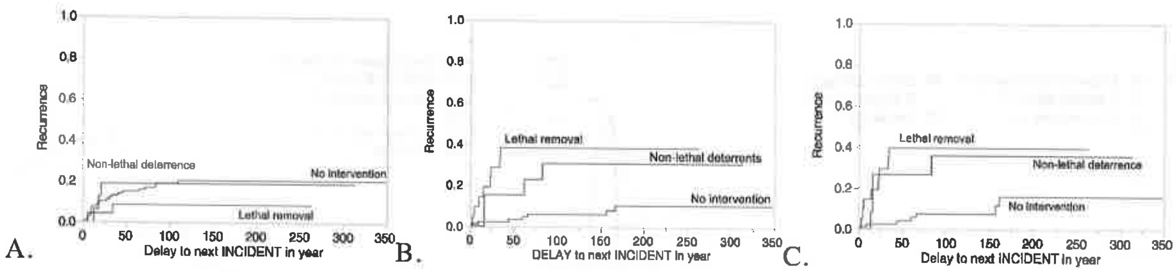

Fig. 2A-C. Recurrence of incidents of wolf-related losses of domestic animals at three scales (A) section (2.56 km^2), (B) township (92.16 km^2), and (C) neighborhood of townships (829.44 km^2) in Michigan from 1998–2014. The x-axis depicts delay to recurrence in days after an original incident and the y-axis depicts the proportion of independent sites with recurrence. Colored lines depict failure rates (1- survival) following three types of government intervention: lethal (red), non-lethal (green), and no intervention (blue). At the section scale (A), 8% of incidents followed by lethal intervention recurred within 5 weeks whereas 19% of incidents followed by non-lethal deterrence recurred after three weeks, and 17% of incidents followed by no intervention recurred after 10–11 weeks. At the township scale (B), 29% of incidents followed by lethal removal recurred within 5 weeks, whereas 28% of incidents followed by non-lethal deterrence recurred after 15 weeks, and 7% of incidents followed by no intervention recurred within 23 weeks. At the neighborhood scale (C), 39% of incidents followed by lethal removal recurred within 5 weeks, whereas 36% of incidents followed by non-lethal deterrence recurred within 13 weeks, and 16% of incidents followed by no intervention recurred within 23 weeks.

Supplementary Material 1: Past research on the effectiveness of lethal intervention to prevent livestock predation

Few lethal interventions have been subject to experimental test using the most rigorous random-assignment of controls and treatments – the gold standard for scientific inference (*51*). The best experiments and quasi-experiments (before-and-after comparisons or nonrandom assignment to treatment and control groups) have been conducted on canid predation on sheep, goats, and cattle.

Although strychnine-laced baits were effective as lethal control for wolves in a before-and-after comparison (*33*), the latter authors recommended more prevention because of the effort and risk of non-target mortality when using a non-selective poison. They also noted the problem that killing only part of a wolf pack prompted disbanding or dispersal by survivors, which could export the problem. Moreover poison is illegal in most wildlife applications and generally considered socially unacceptable, at least in the USA (*21*). With most uses of poison banned, research turned to other, more selective methods of lethal intervention. Correlational studies suggested selective coyote-killing would be needed (*29, 36*). Early field studies (pre-2000) within private livestock operations all suffered from several design limitations that preclude firm conclusion as we explain below.

Experimental and quasi-experimental studies on an experimental sheep ranch with coyotes and other predators showed that virtually only breeding pairs of coyotes attacked sheep, bobcat *Lynx rufus* predation was sometimes misidentified as coyote predation, and non-selective methods often removed non-culprits and missed the breeders (*36, 52-56*).

Guthery and Beasom (1978) reported that high losses of 33–90% (verified–estimated) of Angora goat kids and 0–24% of nanny-goats were reduced by intense lethal control with traps, snares, M-44s, and shooting (some aerial) to 16–59% of kids and 0% of nannies, a result deemed insufficient by the authors (*57*). However the pastures were used for the first time as pasture during the experiment, apparently had no supervision, no shelters were available for the goats, and the untreated site had suffered twice the native prey decline as the treated (lethal control) pasture. The lack of typical supervision (herders or ranchers) was partially offset by the researchers visiting daily to collect data and conduct lethal interventions.

Private working livestock operations present different conditions naturally. O'Gara et al. (*58*) published a before-and-after comparison on a single property where the researchers first attempted to habituate coyotes to observation then later switched to lethal interventions when compensation funds began to run out. It is unclear how habituating coyotes and then killing them affected the results.

Wagner and Conover (*59*) reported a study of montane, sheep pastures subject to summer lethal control. In one set of pastures, coyotes were implicated in lamb losses of 7.3–35.2% (verified–estimated) after being subject to 3–4 other non-selective lethal methods, whereas another set of pastures was treated with those same lethal methods as well as an average of 2.1 hours of winter, aerial gunning. That treatment resulted in 2.7–11.8% losses (*59*). Oddly the article and citations to it suggest it tested the efficacy of lethal interventions – "Preventive aerial hunting from helicopters in winter can be an effective means of reducing sheep losses to coyote predation on summer pastures in mountainous areas." (p. 611, (*59*) – whereas clearly it is a comparison of two lethal treatments. Also the study had 5 deficiencies that were fatal to the conclusions. (1) A large difference in lamb and ewe densities is obvious in their Table 2 (*59*), in which untreated pastures averaged 72 sheep km^{-2} compared to treated pastures that averaged 51 sheep km^{-2}. Higher densities of livestock have repeatedly been shown to be more vulnerable to predation (*60-63*). (2) Pre-treatment sheep losses were 186% higher in untreated then treated pastures (average per pasture $year^{-1}$: 5.4 vs. 2.9) so there was selection bias in the subsequent treatments. (3) Untreated pastures were subject to twice the non-gunning, lethal control effort using snares, traps, and M-44s (*59*). (4) Livestock-guarding dogs were apparently matched between treated and untreated pastures but no data were presented to substantiate the claim. (5) The authors made unsupported assumptions that the ratio of known to unknown losses was assumed constant across treatments and years.

More recent experiments with coyote and red fox removal revealed small effects of lethal control. Some reductions were quite small, i.e., 1.5–10.25% (verified–estimated) dropped to 0.9–6.5% with one lethal control operation $year^{-1}$ and 0.2–3.25% with three lethal control operations $year^{-1}$ (*64*).

Studies of selective lethal control of wolves have shown little or no effect. Tompa and Fritts (*35, 65*) working in British Columbia and Minnesota respectively both found low rates of recurrence when no wolves were killed and these were sometimes lower than when wolves were killed. One of the largest quasi-experimental studies of live-trapping wolves to prevent depredation concluded,

> "No analysis indicated that trapping wolves substantially reduced the following year's depredations at state or local levels. However, more specific analyses indicated that in certain situations, killing wolves was more effective than no action (i.e., not trapping). For example, trapping and killing adult males decreased re-depredation. At sheep farms, killing wolves was generally effective. Attempting to trap, regardless of the results, seemed more effective at reducing depredations than not trapping, suggesting that mere human activity near depredation sites might deter future depredations." (Abstract,*66*)

However, the latter authors made decisions and discarded data without clear rationales and made a series of subjective decisions in modeling and data cleaning that we cannot evaluate. For example,

> "We considered multiple depredations at the same farm as separate events unless otherwise noted…Reasons for no trapping varied, so we selected only sites where given reasons would not seem to affect the analysis, such as the following: farmer denied permission, government manpower shortage, lack of funds, poor ground conditions, and too much hunter activity. If the reasons that complaints were not trapped included the following, we did not include them in our no-trapping reference sample: already trapping at a neighboring farm, stock removed from area, lone wolf responsible for depredation, or no reason given…To assess geographical distribution of apparent unsuccessful trapping, we used ArcView … to map locations of depredated farms where trapping was unsuccessful both after single complaints and after multiple trapping events. We hypothesized that such farms might be in the path of dispersing wolves just passing through the area, so they would be located primarily on the edge of each year's depredation minimum convex polygon (MCP)... We then excluded all the unsuccessfully

> trapped farms along each year's MCP edges, allowing us to reexamine the effectiveness of unsuccessful trapping with the potential bias of farms affected by dispersing wolves removed. For complaints received 1 January–30 September, we calculated the percent with no more depredations the rest of the year, hypothesizing that excluding edge farms where no wolves were captured should decrease apparent effectiveness of unsuccessful trapping." (p. 779, *66*)

The most recent, before-and-after comparison over three years found non-lethal controls were more effective at reducing livestock losses (69–74% reductions) and cost less than lethal controls on 11 South African sheep or cattle operations facing lack backed jackals *C. mesomelas* and caracals *Caracal caracal*, as well as leopards *Panthera pardus* on 7 of the 11 farms (*3*). During the lethal control year, all farms used some combination of gin traps, gun traps, or hunters for lethal control and experienced livestock loses of 4.0–45.0% (all verified). During the two non-lethal control years, all 11 farms converted to non-lethal controls (year 1 verified losses 0.1–15.0%, year 2 verified losses: 0.1–14.2%). Unverifiable mortalities were excluded from analysis as is standard in most livestock predation studies. The allocation of the various non-lethal controls (livestock-guarding dogs, alpacas, livestock protection collars) was based on the willingness of the farmer and on local conditions not randomized. The three different non-lethal controls did not differ in cost-effectiveness. All were more cost-effective than the prior lethal controls on that same farm (costs declined an average of 74.6%) and the second year of non-lethal control averaged 13.3% lower predation then the first year of non-lethal control, and also averaged 43.9% lower cost (*3*).

In sum, early conclusions still seem correct that lethal interventions are rarely selective enough to reliably and consistently reduce livestock predation (*31, 36*). More recent evidence suggests even if they are selective the counter-productive side-effects and relative cost-efficiencies must be considered.

Supplementary Material 2: Materials and Methods

The States of Wisconsin (WI) and Michigan (MI) monitored wolves and complaints about wolves annually. We used the federal government's published reports for the states' minimum, late-winter wolf population sizes (http://www.fws.gov/midwest/wolf/aboutwolves/mi_wi_nos.htm accessed 6 December 2014) supplemented by WI and MI annual reports obtained through a Memorandum and Cooperative Grant Agreements to AT, and from the Little River Band of Ottawa Indians' request for data through a federal Consent Decree respectively. The states estimated wolf numbers, numbers of packs, and pack sizes by winter, snow-track surveys, summer howling, and aerial telemetry of VHF radio-collared wolves primarily (*67-69*). The sole exception was 2012 when MI did not census its wolf population so here we interpolated the minimum, late-winter population as the midpoint of the 2011 and 2013 censuses. For MI we did not have the number of packs for all years, so we used the population estimate only. For WI, the numbers of wolf packs population estimates were collinear (r=0.99). Data for packs was more reliable and precise than that for population for several reasons. Population estimates reflected over-winter mortality after most incidents of domestic animal loss that occur from April–October (*13*); also population estimates under-counted loners and showed increasing variance between minimum and maximum bounds over time. Wolf abundance and spatial predictors were measured with error so we report slopes of regressions using total (orthogonal) LSE (*70*) whereas removals were reported without error by law so we report slopes from standard LSE.

From 15 April 1979–14 April 2013 (wolf-years 1980–2013), the State of Wisconsin (WI) verified 496 independent events in which wolves injured or killed 1,262 domestic animals on or near private property, which excluded events involving hunting hounds (hereafter incidents). We evaluated the aftermath of 277 wolf removals including 195 killed following verified domestic animal loss (depredation culling), 44 killed during other government actions involving no damage which were mainly perceived threats to human safety or property (other culling), and 38 removed from private properties and released in wilder areas (translocation) from wolf-year 1979–2012 (Figure 1A). In wolf-years 1995–2013, the State of Michigan (MI) verified 504 domestic animal losses in n=225 incidents from 15 April 1994–14

April 2014, which were then subject to 110 removals (n=57 depredation culling, n=44 other culling, and n=9 translocated, Figure 1B). Neither state had implemented public hunting and trapping during the periods of lethal removal we used above.

Complaints of wolf attacks on domestic animals were verified by the USDA since 1990 (*25*). USDA agents recorded if a complaint represented a verified injury or death of a domestic animal, which sometimes resulted in 'depredation culling', or if it represented a threat to human safety or domestic animal without direct economic loss, which sometimes resulted in 'other culling'. To estimate incidents, we included only verified claims involving injured or killed domestic animals, including pet dogs that were on or near private property and not involved in hunting. The response variable, incidents was a subset of verified complaints selected by two criteria to attain statistical independence. No two incidents could occur in the same 48-h period within the same section (2.56 km^2). Sections can be read from commercially available road atlases that all verifiers used to record field data at the sites of complains in both states. Sometimes more precise GPS locations were also provided but inspection revealed that many of these were simply the latitude and longitude of the center of the section. Therefore we used the section as our smallest analysis and mapping unit. Removals were also carried out by USDA staff in consultation with state agents, with some exceptions described below. Removals involved live-trapping on or near the complainant's property for several weeks after an incident. A live-trapped wolf would then be relocated or killed by gunshot. Up to 7 wolves were killed after a single incident but the mode was one. Of a total of 38 translocated WI wolves, 18 died or were placed in captivity before they could reproduce successfully the next season, four radio signals were lost before next breeding season (presumed dead), and 16 were being monitored after the next bleeding season. We did not have data on the fates of MI's nine translocated wolves.

Incidents in WI fit a Johnson S_L distribution (annual mean = 14.6, sd = 20.1) much better (-2 x Loglikelihood = -2686 than gamma Poisson 237, or negative binomial 237). The parameters associated with the bounded Johnson S_L distribution violate the regularity conditions of maximum likelihood estimation (MLE) and other standard modeling techniques (*71*). Least-squares estimation (LSE) significantly outperformed MLE or Bayesian methods for fitting independent data to a Johnson S_L distribution (*71*). We also used nonparametric and parametric nonlinear correlations for comparison (Table 4). Depredation culling and other culling were not correlated (r = -0.07 and +0.10 in WI and MI respectively). We found logistic fit stronger than quadratic and linear fits (other culling: logistic fit AICc weight 88% verses 8% and 4% respectively; Depredation culling: logistic fit AICc weight 88% verses 8% and 4% respectively). Therefore we ran the multiple regression in Table 2 again with a Poisson GLM with log-link function but the fit was worse (full model AICc=406). Therefore we preferred the linear fits especially because the nonparametric test that linearizes the factors was superior in 7 of 8 tests (Table 1).

We used WI's annual reports for the approximate territories in a geographic information system (GIS) from wolf-years 2000–2011. We calculated total pack area and total pack perimeter for each year using the ArcGIS® spatial geometry calculator. We collected landscape features using the methods described in (*14*) with one addition: a statewide estimate of the number of livestock premises per township (standard geopolitical units of 92.16 km^2).We estimated land cover percentages, overlap with livestock premises at a township scale, and cattle density within counties that varied in size (n=72), by the areal proportion of overlap with the estimated wolf pack territories. Land cover was estimated from 30 m resolution Landsat TM satellite imagery and ground-verified land cover classes (*72*). We could not quantify the number of available domestic animals adequately because these were not censused at the scale of wolf pack ranges. Moreover, we could not reliably discriminate vulnerable domestic animals from invulnerable ones because dairy cattle are rarely vulnerable to wolves yet they are pooled with beef cattle whose calves are wolves' most common domestic prey. Nor were annual county-scale data available for the number of calves, poultry, or farm dogs. Another variable considered important to predict annual livestock predation in our area is winter severity, because wild prey are more vulnerable to wolf predation during severe winters, which might reduce the wolves' need to prey on livestock (*12, 73*). Using annual snow cover area for the Northern Hemisphere (https://www.climate.gov/news-features/understanding-climate/climate-change-spring-snow-cover accessed 15 January 2015), nether snow cover of the previous year nor the same year were significant predictors of the number of incidents in the same year (r=-0.02 and r=0.26 respectively). But five other spatial predictors were significant predictors: total perimeter of all wolf pack territories was the weakest predictor (r=0.53), whereas the number of livestock premises overlapped by pack territories (r=0.76), total pack territory area (r=0.77), and cattle density overlapped by pack territories (r=0.782) were intermediate.

Fine-scaled analyses: At the scales of analyses smaller than the state, we omitted analysis of threats (to people or property in which no damage was done) because those data varied in quality and reporting criteria. There were numerous categories (pet, human, livestock) of threats but evidence in MI's "Wolf Activity Reports" suggested one complainant's 'threat' was another person's 'encounter' that did not result in a complaint, verification, or government intervention. Some threats triggered lethal removal of a wolf for human health and safety concerns but we could not determine the specific criteria used at each field inspection that led to lethal interventions. Considering the potential biasing effects of under-reported threats (false zeroes) and lack of any such reports prior to 2002, we included only incidents as defined for statewide analyses. Similarly for MI we omitted the 32% of lethal removals related to threats, only 5% of which occurred in the same townships (n=2) as our analyses. We conducted fine-scale analyses in MI only because two features of WI's lethal interventions clouded our analyses. First during at least two periods between 2005 and 2013, WI landowners were issued permits to shoot wolves on their property but we could not ascertain from the resulting reports whether executing those permits followed real or perceived damages. Such removals were treated as depredation culling in the interannual comparisons but for fine-scale analyses we required an original incident to measure delay to recurrence. Second, WI conducted 'catch-up' interventions by killing wolves on farms with wolf-related losses in the preceding 2 years. The resulting interval between an incident and intervention was so much greater than all other interventions that we opted not to include WI in fine-scale analyses here.

MI wildlife agents responded in several ways to incidents: 'no intervention', 'non-lethal', or 'lethal'. 'No intervention' referred to the agency recording no physical intervention although advice and technical support were nearly always provided and documented in Wolf Activity Reports. 'Non-lethal' included one or more of the following: cracker shells, hazing kits, live-traps, lights, and fencing with flags or other materials. If traps were set but no wolves captured, we classified the intervention as non-lethal. 'Lethal' consisted of killing one or more wolves, usually live-trapped wolves killed by gunshot on or near the property with an incident. We included only lethal removals following verified depredations of livestock not threats or fenced wild cervids. We did not include the public hunting season at the end of 2013 because those removals were not focused precisely on incident sites and we could not connect hunted wolves to a prior depredation with confidence: "Most of the wolves killed during the recent hunt in Michigan's Upper Peninsula probably belonged to packs that have caused problems for people… state wildlife biologists say." ((*74*) accessed 15 January 2015 at http://archive.freep.com/article/20140126/NEWS06/301260120/michigan-wolf-hunt-DNR). Because of our criteria for independence and repeated trapping efforts at some sites, multiple wolves might be caught and killed after an original incident. Therefore, we tested whether killing multiple wolves or the interval between the original incident and first capture of a wolf correlated with delay to recurrence.

From Wolf Activity Reports that included 260 verified complaints of wolf-related losses, we extracted 166 independent incidents, i.e., 94 verified complaints occurred <48 h after a prior complaint in the same vicinity so we combined those into a single incident. The 48-h criterion was conservative because MI compensation rules required a complainant to report within 24 h of a loss and the USDA verifiers reached virtually all properties within 24 h of a complaint. Also, MI law gives owners 24 h to dispose of animal remains, which could otherwise attract wolves back to the site of a previous kill. Therefore the same carcasses left out for verification might attract the same or new predators if we chose a period <48 h and almost certainly such a short period would precede intervention (lethal or non-lethal). With independent incidents as above, we determined the sequence of events following the first or 'original' incident in its particular vicinity in the same year (Figure S1).

We calculated the delay to recurrence as the interval in days to the next incident in the same vicinity (section or larger geographic unit, see below). If there was no subsequent incident in the vicinity that calendar year, we censored that observation at 31 December of the same year (Figure S1). We also measured the interval between an original and a subsequent incident across the entire study period. At our smallest geographic scale, delay to recurrence did not change over the years (r_s=-0.12, p=0.14) indicating no apparent acceleration or deceleration in depredations over the course of the study. However when censored at the end of the study, delays to recurrence decreased over the years as one might expect because later incident tended to be censored by the end of the study (r_s= -0.73, p<0.0001). Most incident occurred in the period January–August (81%) and only 2% occurred in November or December. Therefore our decision to measure and censor the delay to recurrence within the calendar year provided at least 60 days to detect an effect in 98% of incidents. This decision was conservative because an intervention should be effective quickly to provide relief for the complainants.

We used the geopolitical unit called a section (1 mile^2 or 2.56 km^2) as the smallest mapping unit for analysis. Neither ownership of a pasture nor the tenure status of a complainant was recorded by the state. All livestock pastures were on private property of <1 section in area (average farm size was 0.3 mile^2 or 0.68 km^2 in the Upper Peninsula, MI Agricultural Statistics Service 2012, accessed December 2014). Of 146 sections with incidents, 106 (73%) occurred once, 23 sections recurred 2–5 times each, and 1 section recurred 17 times so it was excluded (see below). Not surprisingly, lethal interventions correlated with the number of incidents in a section (r_s=0.32, p=0.0008). The next larger scale of analysis was the 36 mile^2 township visible in commercial road atlases. Incidents occurred in 64 townships, 32 (50%) only once, 16 (25%) recurred twice, 13 (20%) recurred 3–5 times, and 3 recurred 10–17 times. For analyses, we replaced the fixed geopolitical unit with a circular buffer of the same area (radius 5.416 km, area 92.16 km^2) centered on each original incident and measured delay to the next incident in that buffer vicinity (Figure S1). Because of that centering, we had 90 unique township buffers as units for analysis. Finally our third and largest scale of analysis was the 'neighborhood of townships' (buffer radius 16.25 km, area 829.44 km^2), an area equivalent to 9 contiguous geopolitical townships centered on the original incident (Figure S1). Incidents occurred in 68 unique neighborhood buffers. Neighborhoods as we defined them were larger than the maximum area of any recorded wolf pack territory in the Midwest (*75*). Our three spatial scales allowed us to analyze if intervention at the original incident was associated with delay to the next subsequent incident in the vicinity and detect if displacement of depredations followed interventions.

One farm (Koski) accounted for 17 of 166 (10.3%) original incidents plus 50 verified depredations and 21 wolves killed by MI. The median delay to recurrence at this farm was 19 days. Fourteen of the 17 incidents recurred in the same 4-year period and these preceded another four independent incidents on other farms in the same neighborhood of townships. That farm had livestock and deer carcasses rotting in pastures, neglected livestock, and multiple interventions before legal proceedings began against the owner (http://www.mlive.com/news/index.ssf/2013/11/john_koski_part_1_tour_the_far.html#incart_river_default and http://www.mlive.com/news/index.ssf/2013/11/john_koski_part_2_see_how_the.html#incart_m-rpt-2 accessed 15 January 2015). Therefore we excluded the Koski farm from analyses as an outlier. Had we included it, the median delay for lethal and non-lethal interventions would have decreased by 6 and 5 days respectively and the brief, local effect of lethal removal we found would have diminished to non-significance (section: median test X^2=5.8, p=0.057). Inclusion would also have increased the significance of the survival analysis (p=0.001 for both township and neighborhood). Including Koski farm did not change the conclusions about the association between the number of wolves removed and delay to recurrence (section r_s=-0.10, p=0.59, township r_s=-0.07, p=0.72, township r_s=0.09, p=0.62).

To analyze the effect of lethal interventions on incidents in the same township the following year in MI, we examined 3 potentially confounding variables: wolf abundance, intrinsically high-risk sites, and nonrandom selection of sites for lethal interventions. Wolf abundance was unlikely to confound the test because the number of wolves within a township was unlikely to grow appreciably from one year to the next given stability in pack sizes (*67*) and the necessary reduction in abundance implied by lethal interventions. If anything, wolf abundance would tend to support the straightforward interpretation of our test because losses should decrease simply because the culprits had been removed ostensibly. Second, the following year's incidents might reflect intrinsic risk as well as that year's interventions, not only the prior year's interventions. Prior work showed that landscapes around farms at scales of 23–92 km^2 varied significantly and consistently in risk of depredation over time (*12, 14, 15, 62*). Therefore only the first incident in a year would be expected to be unaffected by subsequent interventions in the same year. That logic suggests the date of the first incident each year should be delayed by lethal intervention. The date of the first incident each year did not vary over the course of the MI study (n=14 years, r^2=0.002, p=0.30), or with snow cover measured in March and April of the same yea (r^2=0.02, p=0.59; data from https://www.climate.gov/news-features/understanding-climate/climate-change-spring-snow-cover accessed 15 January 2015). Snow cover was a potentially confounding variable because the earliest incident might be affected by winter severity (*12*). Then we examined if the date of the first incident in a year was predicted by the number of wolves removed the previous year (tested alone: n=14 years, r^2=0.01, slope=-0.8, p=0.70. or in conjunction with snow cover slope=-0.9, p=0.68). Another potential confounding factor would have been if lethal interventions had occurred significantly more often at farms where recurrence was more likely anyway. That explanation seems implausible because state authority for lethal removal was permitted and rescinded by the federal government independent of its implementation (*19*). Therefore many high-risk sites did not receive lethal removals. Also the outlier farm with the most losses and the most wolves killed (Koski farm above) strengthened the results because delays to recurrence were more rapid than the median and 17 of the incidents at that farm were the first in their neighborhood of townships. Therefore the test of recurrence over 2 years at a township scale appeared uninfluenced by the above potentially confounding variables.

We calculated chi-squared values to compare delay to recurrence across interventions, using two tests. The median test compared the number of points above the median delay to the number below the median. The second test was a survival analysis of 'failure' lines (% recurrence) as a function of delay. The survival analysis was more sensitive to differences over time than the median test (Figure 2A-C). We used Spearman rank correlations (r_s) to correlate delay to recurrence with predictors such as the number of wolves killed, interval to first wolf capture, or year. We used GLM with Poisson fit and log-link functions (MLE) or LSE regressions with AICc to compare multivariate models for before-and-after comparisons.

Figure S1. Schematic of four hypothetical situations depicting INCIDENTS within vicinities of circular buffers with the same area as a township (panels A-C, small, dashed circles) or circular buffers with the same area as a neighborhood of townships (panel D, large, dashed circle). Different polygons represent different interventions (circle=no intervention, square=non-lethal, triangle=lethal). Original INCIDENTS (solid black polygons) are the center of their vicinity surrounding subsequent INCIDENTS (gray polygons). DELAY was calculated as the number of days between an original INCIDENT and the next subsequent INCIDENT in the vicinity. A: The simplest case of an original INCIDENT (April-1) and one subsequent INCIDENT (May-1) in one township-year produces a single observation with DELAY=30 days. B: Two original INCIDENTS and a change in intervention. The first, original INCIDENT on April-1 was followed by no intervention and a subsequent INCIDENT on May-1, which together produces a single observation with DELAY=30 days. The INCIDENT on May-1 is also an original INCIDENT with regard to the subsequent INCIDENT on June-1 because the intervention changes to non-lethal, producing a second observation with DELAY=30 days. The incident on June-1 is not original so it is not censored at the end of the year. C: Three original INCIDENTS. The first INCIDENT on April-1 is followed by no intervention and a subsequent INCIDENT on May-1 that produces the first observation with DELAY=30 days as in A. The INCIDENT on April-15 is another original INCIDENT for two reasons: (1) it lies outside the vicinity of the first original INCIDENT and (2) it was followed by a new intervention (lethal). It is followed by a subsequent INCIDENT on April-30 for an observed DELAY=15 days. Finally the INCIDENT on April-30 is also original because it was followed by a new intervention (non-lethal) but no subsequent INCIDENT follows it in its township-year so DELAY=245 days (censored at 31 December). D: Changing from original to subsequent INCIDENT as scale changes. Although the small dashed circles (townships) overlap, the INCIDENT sites (black or gray-gradient polygons) themselves do not lie within the same township as another INCIDENT. Therefore all three are original in their respective township-years. All three INCIDENTS occur within the same neighborhood of townships (outer circle of long dashed lines) centered on the earliest, original INCIDENT on April-1. The next subsequent INCIDENT (gray-gradient) on May-1 provides a single observed DELAY=30 days. The INCIDENT on May-15 was followed by a change in intervention but no subsequent INCIDENT so it generates another observed DELAY=246 days The sample size declines from 3 to 2 as the scale increased from township to neighborhood.